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THE RATE OF GROWTH AND ECESIS IN LICHENS[1]

BRUCE FINK

One frequently sees statements concerning the rate of growth in lichens; but these are based, with few exceptions, on uncertain observations rather than on measurements. Aside from results obtained in cultures, the exceptions are a few measurements in Lotsy, J. P., "Beiträge zur Biologie der Flechtenflora des Hainbergs bei Göttingen" (1890) and Howe, R. H., Jr., "Aspects of New England lichens" (1908). In order to obtain sufficient data for a safe conclusion regarding the rate of growth and ecesis in lichens, the writer began a series of studies near Oxford, Ohio, and another near Big Hill, Kentucky, during the summer of 1908. At the request of a number of botanists, a preliminary statement about the work near Oxford, Ohio, was given in "Licheno-ecological studies from Beechwood Camp," published in *The Bryologist* for March, 1909. During 8 years ending with the summer of 1916, the lichens under observation had developed to such an extent, for most of the studies, that nothing would be gained by further observation. Therefore, the time has come for a final report, which may be supplemented later by recording further observations from a few of the areas.

The studies near Oxford, Ohio, may be summarized thus: 17 for rate of growth, 18 for rate of primary succession, and 18 for rate of secondary succession. Those near Big Hill, Kentucky, are 20 for rate of growth, 20 for primary succession, and 17 for secondary succession. The succession studies also furnished valuable data on the rate of growth. Of 107 studies begun, 45 are reported herein. For various reasons, the other 62 studies gave no results worth recording. Some of them were destroyed before valuable results could be obtained, while a few ran the whole 8 years without giving data of sufficient value to warrant publication. Some of the succession studies reverted to the conditions surrounding them before the 8 years had expired; 1 was destroyed by erosion; 1 was lost because of poor marking; others were destroyed through human agency; in 2 instances there was total lack of succession on chipped-rock surfaces. Of the studies of rate of growth, some of the plants under observation disappeared through destruction of the substrata on which they were growing, or through various other forms of natural or human interference. In 3 instances the plants ceased to grow soon after they had been marked; in other 3 instances the logs on which the lichens were growing were destroyed; in 5 instances the plants began to deteriorate soon after they had been marked, or possibly before the marking was done; in 4 instances the rocks on which the plants were marked disintegrated rapidly; and in 3 instances the plants appeared healthful for a long period, but failed to grow nevertheless. Though so large a proportion of the studies suffered through various vicissitudes, the 45 reported herein contain data sufficient for our purpose.

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[1] Contributions from the Botanical Laboratory of Miami Univerity,—XIII.

The observations were made in the Ohio area in 7 of the 8 years during which the studies ran, omitting a year after the fifth of the series of observations and another after the sixth. The results proved that the added data scarcely justified the labor involved in making observations so frequently. Consequently, in the Kentucky area, which was reached by a journey of 175 miles, 2 years were allowed to pass without observing after the second series of observations and 3 years after the third series. This gave 7 series of observations for the Ohio area and 4 for the Kentucky area. The dates of observation for the Ohio area are August 4 to 13, 1908; August 1 to 9, 1909; July 31 to August 5, 1910; July 29 to August 3, 1911; July 31 to August 4, 1912; July 11 to 18, 1914; and September 1 to 7, 1916. The dates for the Kentucky area are October 23 to 30, 1908; August 20 to 27, 1909; September 3 to 6, 1912; and August 24 to 26, 1916. Ten of the studies in Ohio were begun in 1909. Only 6 observations were made on these.

The number of sets of data for each study recorded below corresponds with the number of observations that showed changes worth recording, before the study was destroyed in some manner, before it reached a stage of development after which further study was of no value, or before the observations were completed for the series as a whole. In the Ohio area, where the observations were made more frequently than was necessary for most of the studies, the number of sets of data for each study often does not reach the number of observations made. In the Kentucky area, the number of sets of data recorded for each study usually reaches the whole number for the area, except when the study was destroyed in some manner.

Where 2 or 3 studies lay side by side on a substratum, the same number was used for the areas, followed by (*a*) or (*b*) to indicate the second or the third of the series lying contiguously. In the Ohio area, 2 sets of numbers were used, unfortunately, 1 for the studies of rate of growth and the other for the succession studies. This accounts for the duplication of numbers for this area.

The areas are grouped below, not according to locality, but according to character of the studies and after this according to the plants involved, passing from lower to higher with respect to somatic structure.

Such expressions as 25 by 31 cm. across refer to a minimum and a maximum distance across the plant and indicate nothing regarding the form of the plants involved.

Statements regarding shade caused by trees refer of course to conditions while the leaves were on the deciduous trees.

Lichen rhizoids are known to penetrate from 0.02 to 1.4 cm. into rock; but the algal-host cells have never been found deeper than 0.5 mm. Though the rhizoids may have penetrated deeper in some instances than the rocks were chipped in our areas tabulated under primary successions, the algal hosts were certainly removed in every instance. Consequently, any remnants of the lichen rhizoids that may possibly have been left in the rocks in any instance, through failure to chip deeply enough, probably died, and the successions recorded as primary are all of this character beyond reasonable doubt.

RATE OF GROWTH

Ohio, area 20, on the north side of a tulip tree 22 cm. in diameter, in a low, shady wood. A well-fruited specimen of

Graphis scripta, situated 1.3 m. from the ground, was 2 by 3.5 cm. across. After 1 year the plant was 3 by 4 cm. across.

Ohio, area 5, on the north side of a maple tree 16 cm. in diameter, growing along the north side of a high wood, where shaded except late in the afternoon. A well-fruited specimen of *Graphis scripta,* situated 1.6 m. from the ground, was 1 cm. across. After 1 year the plant was 1.2 cm. across. After 2 years it was 1.5 cm. across.

Ohio, area 21, over a mossy rock along a brook, in a low, moist wood, well shaded. A specimen of *Peltigera canina* 10 by 14 cm. was deprived of several large apothecia. The lobes all pointed in the same direction, and the plant grew 1.75 cm. in this direction in 1 year. The area deprived of its apothecia produced 12 young apothecia, of which only 1 was sufficiently developed at the end of the first year to show the brown disk. From 2 plants near by, the lobes were all removed, leaving the plants 2 and 5 cm. across the longest way. After 1 year the lobes were so completely regenerated that one would not know that they had been amputated. The plants were, at this time, 3.5 and 6 cm. across the longest way.

Kentucky, area 1, a quadrat 10 cm. square, situated on a sandstone ledge about 200 m. above the surrounding country, the dry rock face making an angle of 45 degrees with the horizon, and exposed to the sun during the middle of the day. Thirty plants of *Umbilicaria pustulata* were measured. After 10 months 1 minute, smooth, sterile plant had increased from 1 to 3 mm. in average diameter, while other smooth, sterile plants had increased as follows: 1 to 2 mm., 5 to 6 mm., 6 to 7 mm., 3 to 3.1 mm., 2 to 2.4 mm., 8 to 9 mm., and 6.5 to 9 mm. There were no fruited or conspicuously pustulate plants in the quadrat at this time. After 8 years the plants that remained in the quadrat were stronly pustulate and bore many apothecia. Many of the plants marked in the first study had disappeared, and younger plants had appeared in their places.

Ohio, area 4, on next to the top rail of a fence along the north border of a high, dry wood, well shaded except late in the afternoon. A smooth and sterile specimen of *Parmelia borreri* 25 cm. in diameter was marked. After 1 year the plant was 26.3

cm. in diameter and showed a few isidioid branchlets. During the second year the increase in size was about the same, and the central, oldest portion of the plant had developed many isidioid branchlets.

Kentucky, area 31, on a sandstone boulder on high, open ground, the boulder 1 by 1.5 m. across, 1 m. high, the upper surface making an angle of 10 degrees with the horizon and facing southward. Five plants of *Parmelia conspersa,* growing on the upper surface, were marked. They varied from 1 to 2 cm. across. After 10 months the plants varied from 1.5 to 2.2. cm. across. After 4 years the sizes ranged from 2.5 to 4 cm. across.

Kentucky, area 3, on the northwest side of the perpendicular face of a sandstone-conglomerate outcrop 2 m. high, standing on a high, dry, sparsely-wooded hill, where shaded until the middle of the afternoon. Two plants of *Parmelia conspersa* 40 cm. from the ground and 1 and 3 cm. across respectively were marked. After 10 months they had increased to 1.5 and 3.5 cm. across. After 4 years the plants were 3 and 7 cm. across. Both specimens were sterile throughout the 8 years of observation, and they did not grow perceptibly during the last 4 years.

Kentucky, area 6, habitat similar to Kentucky, area 3,[2] but the plants 75 cm. from the ground. Two specimens of *Parmelia conspersa* were marked, both sterile and smooth, and 1.4 and 4 cm. across, respectively. After 10 months the plants were 2.5 and 5 cm. across. After 4 years they were 3 and 8 cm. across. The plants remained smooth and sterile during the 8 years of observation; and they deteriorated toward the close of the period so that further observations could not be made.

Ohio, area 19, on a tulip tree, 22 cm. in diameter, in a low, moist wood, furnishing shade. A smooth and sterile *Parmelia caperata,* situated 1.4 m. from the ground, measured 3.5 by 4 cm. across. After 1 year the plant was 3.75 by 4.8 cm. across and still smooth and sterile.

Ohio, area 6, habitat similar to Ohio, area 5,[3] but 1.4 m. from the ground on the northwest side of the tree. The specimen of *Parmelia conspersa* studied was 1.5 cm. across when marked.

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[2] See the area discussed next above.

[3] See Ohio, area 5, p. 141.

After 2 years it was 2 cm. across in one direction and 2.4 cm. across at right angles. After 3 years the plant was 2.6 and 2.9 cm. across in the 2 directions respectively.

Ohio, area 7, habitat similar to Ohio, area 5,[4] but only 0.2 m. from the ground on the north side of the tree by a little east. The specimen of *Parmelia conspersa* studied was smooth and sterile and 1 by 1.6 cm. across. After 1 year the plant was 1.3 by 1.9 cm. across. After 2 years it was 2.1 by 3 cm.; after 3 years, 3.5 by 4.1 cm.; after 5 years, 4.5 by 5 cm.; after 7 years, 7 by 8 cm.; and after 8 years, 10.2 by 12.9 cm. across. After 7 years the central portion of the thallus, about 2 cm. across, bore scattered isidioid branchlets, which increased in number and area covered during the following year.

Ohio, area 3, on next to the top rail of a fence, well shaded by a mesophytic wood, except late in the afternoon. A smooth and sterile specimen of *Parmelia caperata* 1.2 cm. across was marked. After 1 year the plant was 1.75 cm. across. After 2 years, 3 by 3.5 cm.; after 3 years, 5 cm.; after 4 years, 5.7 by 6.5 cm.; after 6 years, 7.3 by 9 cm.; and after 8 years, 10 by 13 cm. across. At the conclusion of the observations the central portion of the thallus half way to the margins was thickly covered with isidioid branchlets.

Ohio, area 1, on the northwest side of a rail lying on the ground, along the north border of a high, dry wood, well shaded except late in the afternoon. A quadrat of *Cladonia pityrea* 10 by 16 cm. was marked. No podetia were present in the quadrat, and the horizontal thallus consisted of small or minute, scattered squamules, many of them too small to be seen with the eye. After 2 years the quadrat was thickly covered with squamules of normal size for the species, and many podetia had appeared. A large proportion of these were detected under the hand lens, but 19 were visible to the eye and varied from 2 to 4 mm. long.

Ohio, area 22, on a hornblende boulder 2.5 by 4 cm., and 2 cm. high, the upper surface facing westward at an angle of 30 degrees with the hroizon and well shaded, except for an hour shortly before mid-afternoon. A specimen of *Physica pulverulenta* and one of *Parmelia conspersa* were marked. The plants were 2.4 by

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[4] See Ohio, area 5, p. 141.

2.7 cm. and 1.9 c.m across respectively. After 1 year the *Physcia* was 2.75 by 3.1 cm. and the *Parmelia* 2.65 cm. across. After 2 years the *Physcia* was nearly circular and 3.6 cm. across, and the *Parmelia* was 3.5 cm. across. After 3 years the *Physcia* was 3.7 by 4 cm. and the *Parmelia* 4.3 by 4.7 cm. across. An area 0.5 cm. across near the center of the *Parmelia* had disappeared. After 5 years the *Physcia* was 4 by 4.45 cm. and the *Parmelia* 6 by 6.5 cm. across. After 7 years the *Physica* was 5. cm. and the *Parmelia* 9.5 by 10.4 cm. across. At 5 years the lost area of the *Parmelia* had increased to 1 cm. across, but at 7 years it was completely regenerated. Both plants were sterile throughout the time of observation.

Ohio, area 16, on the trunk of a beech tree 20 cm. in diameter, standing in a low, shaded wood. An area of *Amphiloma lanuginosum* 3.3 by 4.1 cm. across was marked. After 1 year the area had increased in size to 3.47 by 4.4 cm., but did not look thrifty. The area was found to be in a dying condition at the time of the next observation.

Kentucky, area 10, on a sandstone block 28 by 35 cm., and 10 cm. high, lying in a high, dry, open wood. Fourteen areas of *Verrucaria muralis* were marked, the largest 2.12 by 2.4 cm. across, the others averaging from 0.4 to 0.5 cm. across in various directions. After 10 months the largest plant was 2.2 by 3 cm. across, and the others averaged from 0.5 to 0.9 cm. across in various directions. The boulder disappeared before the time for the next series of observations.

SECONDARY SUCCESSIONS

Kentucky, area *7a*, habitat like Kentucky, areas 6 and 7.[5] The thallus of *Amphiloma lanuginosum* was scraped from the rock over a circular area 10 cm. in diameter until no remnants were visible to the eye. The area about the study was left with the thallus of the same plant undisturbed. After 10 months there was no evidence of ecesis. After 4 years the thallus was returning over numerous centers from 0.5 to 2 mm. across. After 8 years the returning areas covered about half of the study and varied from 2 to 30 mm. across. At this time the study differed in appearance from the surrounding undisturbed area only in that the areas of thallus were more scattered.

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[5] See Kentucky, areas 6, p. 142, and 3, p. 142.

Kentucky, area 4a, habitat like Kentucky, area 4.[6] All the apothecia of *Biatorella simplex* were taken from a quadrat 5 cm. square, using the hand lens to get the smallest ones and taking also a large proportion of the epilithic parts of the thallus. After 4 years the quadrat showed numerous apothecia, some of which were 1.5 to 2 mm. in diameter.

Kentucky, area 21, on the flat top of a sandstone block near the top of a high, dry hill, the block 1 by 1.4 m., 1.3 m. high, and lying in the sun for 4 or 5 hours near the middle of the day, but shaded during the remainder of the day by a high cliff on one side and by trees on another. A quadrat of *Ramalina calicaris* was laid out 1.5 cm. square, and the *Ramalinae* were all removed, except basal remnants about 0.1 mm. long. After 10 months several plants were found that showed no evidence of having been cut off, varying in size from those too small to be seen without the hand lens to others 0.1 to 0.2 mm. long. After 8 years there were 6 plants from 2 to 5 mm. long, all sterile.

Kentucky, area 27, at the edge of a high, dry cliff facing northward, partially shaded in the forenoon by shrubs to the south. The center of a thallus of *Parmelia conspersa* 28 by 33 cm. was taken out over an area 20 by 25 cm. across, except small fragments not easily detached from the rock. Ten areas 1 to 2.5 cm. across and many other minute areas were left. After 10 months the marginal zone of the thallus had grown outward until the distance from one side of the margin to the opposite side was 29 and 34 cm. in the two directions in which the thallus had been measured previously. The inner border of the marginal zone left undisturbed showed numerous lobes regenerated and extending inward, these lobes varying in length from 1 to 15 mm. The areas left in the denuded center showed regenerated lobes about their margins, varying in length from those barely visible under the hand lens to others 3 mm. long. Also there were many minute thalli arising over the denuded center, varying in size from those only discernible by aid of the hand lens to others from 0.5 to 1 mm. across.

[6] See Kentucky, area 4, p. 151.

These probably arose from minute remnants of the thallus left in scraping the central portion of the plant from the rock. After 4 years the areas returning over the denuded center had increased in size considerably and were beginning to overlap. After 8 years a dozen regenerated thalli had covered the denuded center, except the portions covered by the regenerated lobes which had grown inward from the marginal zone not denuded to meet and overlap these. The 12 thalli varied from 2 to 5.3 cm. across. At this time the whole area was 32.3 by 40.4 cm. across.

Kentucky, area 30, 1 m. from the top in a crevice 1.5 m. wide and extending nearly north and south through the face of a high, dry, northward-facing cliff, the crevice shaded, except near the middle of the day. The thalli of *Umbilicaria pustulata* and *Gyrophora dillenii* were removed from a circular area 4 dm. in diameter, except a few fragments about 1 cm. across, left attached by the umbilici, and 9 specimens of the former plant of about the same size. Plants of the same species were left about the study, and some of those of *Umbilicaria pustulata* bore apothecia. After 10 months the fragments showed no evidence of regeneration, and the plants left had not grown sufficiently so that any increase in size could be noted. After 4 years 15 plants were found growing in the area; but it was not possible to determine which might have arisen from regeneration and which might have represented the minute plants left when the study was plotted. The largest plant was 3.8 by 4.2 cm. across, and this and two other plants of *Umbilicaria pustulata* were sparingly covered with pustules. The other 12 plants were from 0.3 to 2.1 cm. across. After 8 years about 40 plants of the two species were found growing in the area. Fourteen specimens of *Umbilicaria pustulata* averaged 2.5 to 5 cm. across in various directions and were conspicuously pustulate. Six of them showed young apothecia from 0.2 to 0.4 mm. across. Twelve specimens of *Gyrophora dillenii* were 1.5 to 3.45 cm. across.

Kentucky, area 13, on top of a limestone rock 0.9 by 1 m. across and 20 cm. high, on a partially shaded, dry hillside, the upper surface of the rock making an angle of 60 degrees with the horizon. All the large specimens of *Dermatocarpon miniatum* were taken from a quadrat 17 cm. square, leaving many small thalli averaging 0.25 to 9 mm. across in various directions. Some of the plants were in groups of 2 to 15 or 20; and the individual plants of the groups were often too small to be seen without the hand lens. All the plants left were sterile. After 10 months the plants had grown but little, the largest one being but 11 mm. across. After 4 years 1 plant was found 13.7 by 14.3 mm. across and another 11.3 by 12.5 mm. across. The remainder of the plants averaged for most part from 0.4 to 1.5 mm. across in various directions. All were still sterile.

Ohio, area 13, a quadrat 19 cm. square, plotted on a boulder 0.7 m. high, 2 m. from a brook in a damp wood. The quadrat was thoroughly scraped with a knife blade, and only minute particles of *Physcia endochrysea*, *Leptogium lacerum*, and the small number of mosses and leafy hepatics interspersed were left adhering to the surface of the rock. After 1 year *Physcia endochrysea* was returning in 30 areas, varying in size from those barely distinguishable under the hand lens to others 1 mm. across. *Leptogium lacerum* was returning in several spots in the quadrat; but the plants were visible only under the hand lens. Bryophytes were also returning and gave a green coloration to portions of the quadrat not covered by lichens; but their gross structure was distinguishable only under the hand lens. After 2 years *Physcia endochrysea* was found growing in 60 spots in the quadrat; and the plants varied from 0.2 to 1.5 cm. across. Some of them were visible 60 m. distant. The other plants showed little change. After three years the largest *Physcia endochrysea* was 1.75 cm. across, and 10 others were 1 cm. across or larger. The bryophytes covered a considerable portion of the remaining area, and the plants were as large as those surrounding the quadrat. The remainder of the quadrat was covered mainly by *Verrucaria nigrescens* sparsely fruited. Poorly developed thalli of this lichen were probably present when the quadrat was plotted, but were covered by other lichens and bryophytes and grew rapidly only after the cover plants had been removed. At this time and at later periods only 3 or 4 minute centers of *Leptogium lacerum* were found within the quadrat. After 7 years *Physcia endochrysea* and the bryophytes covered about three-fourths of the quadrant in approximately equal areas, and *Verrucaria nigrescens* had taken the other one-fourth. The quadrat had reverted to conditions found over the remainder of the rock; for *Leptogium lacerum* had largely disappeared, while *Verrucaria nigrescens* had become conspicuous without the quadrat as well as within it. The *Physcia* was sterile both within and without the quadrat.

Kentucky, area 12, on the upper surface of a boulder 80 by 140 cm. and 30 cm. high, lying on a dry hillside, the upper surface making an angle of 35 degrees with the horizon and exposed to the sun, except during half of the forenoon. A small area of *Psora russellii* was stripped of apothecia. After 10 months the area showed 2 small apothecia. After 4 years 50 apothecia were found, some of them of average size for the species. After 8 years more than 100 apothecia were present.

Kentucky, area 14, a quadrat 30 by 40 cm. on a limestone rock 40 by 100 cm. and 75 cm. high, lying in an open, dry wood where poorly shaded, the upper surface making an angle of 15 degrees with the horizon. *Leptogium lacerum* and the moss on which it was growing were rubbed and scraped from the rock, except bits of the moss and particles of the lichen which adhered to the rock, especially in depressions of the rock surface. After 4 years the moss was found returning over 300 or more small areas, many of them bearing specimens of *Leptogium lacerum* 2 to 10 mm. across. Very little change occurred during the next 4 years.

Kentucky, area 25, a quadrat 32.5 by 45 cm. at the top of a high, dry cliff facing northward, the quadrat on bare rock at the edge of the cliff, but on soil 16 cm. deep at the opposite side, partially shaded during the forenoon by low shrubs. Many plants of *Cladonia uncialis, C. cristatella, C. fimbriata,* and *C. pyxidata* were torn and pounded from the *Polytrichum* on which they were growing, and the fragments were strewn over the quadrat. After 4 years *Cladonia uncialis* and *C. pyxidata* were both abundant and well developed with many podetia of normal form and size. After 8 years the 2 lichens had taken the quadrat, and about one-fourth of the podetia of *Cladonia pyxidata* bore apothecia.

Kentucky, area 24, habitat similar to Kentucky 25,[7] but back 2 m. from the edge of the cliff, on soil 0.5 m. deep over the rock. The quadrat, 10 by 14 cm., was covered by *Cladonia uncialis* growing over mosses. The *Cladonia* was removed as thoroughly as could be done over part of the quadrat, while over the remainder of its surface the upper half of each podetium was cut off, leaving the basal portion 1 to 1.5 cm. long. Over the portion from which the plants had been removed as completely as possible, the podetia were broken into small or minute fragments and worked into the mossy substratum to test the rate of regeneration. After 4 years the plants were regenerated, and *Cladonia uncialis* was as luxuriant as over surrounding undisturbed areas. The regenerated plants were particularly luxuriant over the portion of the quadrat on which the fragments had been worked into the substratum.

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[7] See the area discussed next above.

Ohio, area 10, a quadrat 10 cm. long on the third rail from the top of a fence in a mesophytic wood, well shaded during the forenoon and partially shaded during the afternoon. *Cladonia pityrea* covered the quadrat, and the podetia and as much as possible of the squamules were removed that the rate of ecesis or regeneration might be studied. After 1 year squamules had developed strongly, and two minute podetia were visible to the eye. After 3 years the quadrat showed many podetia from 3 to 5 mm. long.

Ohio, area 11, a quadrat 65 cm. long on the upper side of the second rail from the top in a fence along a roadside in a mesophytic wood, well shaded in the forenoon and partially shaded during the afternoon. All visible portions of the 3 or 4 species of *Cladonia* which covered the quadrat were removed, leaving the rotted surface of the rail. After 1 year squamules were returning over most of the quadrat and were of sufficient size and number to be seen at a distance of 3 m. After 3 years 40 podetia were present in a small portion of the quadrat. These were 3 to 4 mm. high, and most of them bore cups.

Kentucky, area 5a, habitat like Kentucky, areas 3 and 5. The thallus of *Cladonia subsquamosa* was taken from a quadrat 5.5 by 1.75 cm., leaving only such fragments as could not be removed from the rock surface. After 10 months a few squamules could be seen in the quadrat. After 4 years the squamules had reached normal size and number, and 50 podetia were developing. After 8 years the podetia as well as the squamules were as numerous and as large as those in surrounding undisturbed areas.

Kentucky, area 5b, habitat like Kentucky, areas 3 and 5.[8] All the podetia of *Cladonia subsquamosa* were removed from a quadrat 2 by 4.5 cm., but the squamules were left. After 10 months 35 short podetia were detected. After 4 years the podetia were numerous and of normal size.

Ohio, area 23, on the top 3 rails of 24 rail-lengths of fence, the rails mostly of sound tulip-poplar and placed in the fence in October, 1908, the area lying along a roadside where exposed to the sun, except under 2 large beech trees where shaded until mid-afternoon. After 2 years 2 minute specimens of *Parmelia tiliacea* were found on a new rail under one of the beech trees. After 6 years several *Physcia tribacia* plants were found on a new rail under one of the beech trees, the largest *Physcia* 5 by 7 mm. One *Parmelia* found 4 years before was now 2 cm. across. On another new rail under one of the beech trees, a strip of *Cladonia* squamules was found scattered over the rail for a distance of 10 cm. On a new rail exposed to the sun was found a *Cladonia* with several minute podetia. One of the new, exposed, top rails showed the thallus of *Placodium microphyllimum* scattered over the whole length of the rail. After 8 years the largest *Physcia tribacia* was 2.5 cm. across, the larger *Parmelia tiliacea* was 6 cm. across, and *Placodium microphyllinum* was found on several new rails scattered along the whole 24 rail-lengths. The last plant bore several apothecia.

Kentucky, area 23, a quadrat of soil 60 by 70 cm., denuded 3 cm. deep and some sticks devoid of lichens scattered over the quadrat, which was poorly shaded by a dry, open wood. The quadrat, before being denuded, was covered by the following plants: several areas of *Cladonia subcariosa*, an area of *C. cervicornis*, some crustose lichens on small stones, and a few mosses which covered the small proportion of the soil not covered by the *Cladoniae*. After 10 months *Cladonia* squamules were beginning to appear on the soil throughout the quadrat. These were large enough to be seen plainly with the eye. Unfortunately, the quadrat was destroyed before another observation could be made.

Kentucky, area 8, an eastward-facing ledge of conglomerate sandstone 4 m. high, lying on a high, sparsely-wooded hill, partially shaded by shrubs on the east and by the rock face on the west, the rock projecting over the area, which is seldom reached by rain. Over a circular area of *Lecanora frustulosa* 10 cm. across and 1.8 m. from the ground, the apothecia and most of the epilithic portion of the thallus were scraped from the rock, using the hand lens to get minute apothecia and fragments of thallus. No development was detected until 8 years had passed when several small areas of thallus and a few apothecia 0.2 to 0.25 mm. across were found. The hardness of the substratum and the lack of moisture probably account for the unusually slow rate of development.

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[8] See Kentucky, area 5, p. 154, and Kentucky, area 3, p. 142.

PRIMARY SUCCESSIONS

Ohio, area 15, a limestone 3.5 by 5.5 cm., largely imbedded in the soil on a northward-sloping, mesophytic hillside, the rock surface level with the soil to 2 cm. above, exposed to the sun. The upper surface, covered mainly by *Pannaria nigra* and a moss, was chipped on the side raised above the soil 1 to 2 cm. deep over a quadrat 2 by 4 cm. After 2 years 4 minute areas of *Pannaria nigra* were found within the quadrat, 2 of which bore one minute apothecium each. After 5 years many more minute lichen thalli were found in the quadrat, but they were too young to be identified. After 7 years a half dozen areas of *Pannaria nigra* were found. Apothecia were few in number. The largest thallus was 1 cm. across and bore 6 well-developed apothecia. The largest of these was 0.5 mm. in diameter.

Kentucky, area 4, habitat like Kentucky, area 3.[9] In an area of *Biatorella simplex,* a quadrat 10 cm. square was made by chipping the rocks 2 to 10 mm. deep. After 4 years many minute areas of thalli were found within the quadrat. After 8 years many minute apothecia were observed under the hand lens. The largest apothecia were 0.25 mm. across, while the largest in undisturbed areas surrounding the quadrat were 2 mm. across.

Kentucky, area 2, on a limestone 8 by 11 cm., lying on dry soil near the top of a steep, wooded hill about 200 m. high, the upper surface of the limestone lying in a horizontal plane, with one of its sides level with the soil while the opposite side was 9 cm. above the soil. *Verrucaria rupestris, Staurothele diffractella, Pyre-*

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[9] See Kentucky, area 3, p. 142.

nopsis schaereri, Placodium sideritis, Collema pustulatum, and *Physcia obscura* (?) were growing on the upper surface of the rock, from which the front one-fourth and the back one-fourth were chipped 2 to 15 mm. deep. After 4 years many minute primordia of lichen thalli were found under the hand lens, within the chipped quadrats. After 8 years these quadrats were sprinkled over with minute thalli of *Pyrenopsis schaereri,* a few small thalli of *Physcia obscura* (?), and several minute and sterile ones of *Collema pustulatum.* All of these thalli were sterile; but a single specimen of *Placodium sideritis* 1.5 cm. across bore 4 minute apothecia.

Ohio, area 7, on a limestone 65 by 5 cm. and 35 cm. high, standing nearly erect in a moist, shady wood, the quadrat covering half of the 65 cm.-wide, nearly perpendicular rock face, chipped 4 to 18 mm. deep. After 2 years all of the chipped quadrat showed an indistinct green coloration, in which the hand lens revealed scattered areas turning toward the dark color characteristic of *Verrucaria nigrescens,* which had covered most of the rock surface before the quadrat was plotted. After 6 years this lichen was found over more than half of the chipped quadrat with numerous apothecia, and thallus nearly as dark as on surrounding undisturbed areas.

Kentucky, area 7, habitat like Kentucky, area 6.[10] In an area covered by *Amphiloma lanuginosum,* a circular portion 10 cm. in diameter was chipped 1 to 10 mm. deep. After 4 years the *Amphiloma* was found returning in patches averaging 0.5 to 2 mm. across in various directions and scattered over the whole area. After 8 years the plant covered about three-fourths of the surface, and a considerable number of larger patches ran from 5 to 10 mm. across in various directions.

Ohio, area 8, from a levee 1.3 m. wide and 0.3 m. high, lying 9 m. from a brook, on usually dry ground exposed to the sun, the limestone fragments composing the levee of sizes easily handled, removed a portion 70 cm. long and replaced it by similar limestone fragments taken from the bed of the brook and devoid of plant growth that could be detected. After 3 years thalli of *Endocarpon pusillum* 0.2 to 2 mm. across were found in considerable abundance on one of the rocks and more sparingly on others. Other thalli were supposed to be the same, but were too immature to be determined. Over most of the replaced portion of the levee, the thalli could be seen only under the hand lens; but at a few points, the darker coloration of the rock could be detected in passing. None of the plants bore apothecia. After 4 years a few of the thalli of *Endocarpon pusillum* showed apothecia; and hundreds of apothecia of *Placodium aurellum* were scattered over some of the rocks. After 6 years the *Endocarpon* had developed many apothecia; and one could easily detect the coloration of the rocks, due to its thallus, from a standing position 8 m. distant. The *Placodium* apothecia had not increased greatly in number. Eight apothecia of *Lecanora dispersa* were seen on one rock. After 8 years the coloration due to the *Endocarpon* thallus could be seen easily over much of the rock when standing 20 m. distant. The apothecia of the *Placodium* were much more numerous, but would be noticed only under the hand lens. The apothecia of the *Lecanora* were still rare and, excepting one group which was easily visible from a standing position, were readily visible only under a hand lens. The thalli of the last 2 lichens could be seen only by aid of the lens.

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[10] See Kentucky, area 6, p. 142.

Ohio, area 12, a soil quadrat 1 m. square on high ground in an open wood, denuded 5 cm. deep, removing all plant parts, except roots of seed plants which extended deeper into the soil and could not be pulled out. The quadrat, before being denuded, was covered by lichens and mosses, with about 85 herbs and 2 seedling trees scattered about within its limits. *Cladonia furcata* was the only abundant lichen. *Cladonia pyxidata* was present in several small patches, and a small cluster of *Cladonia mitrula* was seen. After 1 year 36 clusters of *Cladoniae* were noted within the quadrat, all so small as to be visible only on careful observation and too rudimentary to be determined. Herbs, mosses, and seedling trees were also appearing. After 5 years the quadrat had reverted to the conditions found in the surrounding area so far as the lichens were concerned. *Cladonia furcata* was again dominant and of the same size and appearance within as without the quadrat.

Kentucky, area 26, habitat like Kentucky, area 25,[11] a soil quadrat 3 by 7 dm., denuded 5 cm. deep, removing the lichens and the superficial portions of the *Polytrichum* on which these were growing. *Cladonia pyxidata* and *C. cristatella* were abundant, and 4 other *Cladoniae* were seen in small quantities. After 2 months many small *Cladonia* squamules were observed in the quadrat. After 4 years a considerable number of specimens of *Cladonia pyxidata* of normal size were observed. After 8 years the quadrat had reverted to the conditions surrounding it. *Cladonia pyxidata* was abundant with 300 podetia within the quadrat. More than 30 podetia bore apothecia. A small amount of *Cladonia cristatella* was present and bore apothecia sparingly. Smaller amounts of 3 or 4 other *Cladoniae* were seen.

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[11] See Kentucky, area 25, p. 148.

Kentucky, area 5, habitat like Kentucky, area 3,[12] a quadrat 4.5 by 5.5 cm., denuded 2 to 10 mm. deep. The quadrat was covered by *Cladonia subsquamosa,* which also grew on the surrounding rock. After 10 months *Cladonia* squamules were detected in considerable number within the quadrat. After 4 years the squamules had increased considerably in size and number. After 8 years squamules of normal size covered one-fourth of the quadrat and bore 20 fully developed podetia. Nearly all of these podetia bore apothecia. Many smaller pedetia were seen.

Kentucky, area 28, habitat similar to Kentucky, area 27,[13] but back 1 m. from the edge of the cliff where more shaded. A quadrat 3 by 4 dm. on soil 3 dm. or more deep was denuded 4.5 cm. deep. *Cladonia pyxidata* and *C. cristatella* in large quantity and *Cladonia verticillata* and *C. squamosa* in small quantity nearly covered the mossy substratum, A small amount of *Polytrichum,* a half dozen low huckleberry bushes, 3 or 4 clumps of grass, and a few other herbs were present. All plant parts were removed from the quadrat, except such roots as extended below the depth of denudation and could not be pulled out. After 10 months many small *Cladonia* squamules were found growing within the quadrat, and about the margin were clusters of larger squamules which bore podetia. These had been carried into the quadrat in some manner. After 4 years *Cladonia pyxidata* was present in large quantity. The squamules were scattered over the whole quadrat, and a considerable number of podetia of normal size were present. The other *Cladoniae* were present in small numbers.

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[12] See Kentucky, area 3, p. 142.

[13] See Kentucky, area 27, p. 145.

Kentucky, area 29, habitat similar to Kentucky, area 28,[14] but 10 m. distant from this and 3.5 m. back from the edge of the cliff in soil of considerable depth. A quadrat 4 dm. square was denuded 5 cm. deep. Growing in the quadrat were 3 greenbriers, 3 huckleberry bushes, 2 seeding pines, a few clumps of grass, a conspicuous covering of *Cladonia cariosa* with few podetia and apothecia, and a few well-developed plants of *Cladonia cristatella* and *C. uncialis*. After 10 months many small *Cladonia* squamules were found scattered over the quadrat. After 4 years the squamules were of larger size. After 8 years the squamules had covered a large proportion of the quadrat, and 25 podetia of *Cladonia cariosa* were counted, some of which were of normal size.

Ohio, area 9, on a new plane-tree board, next to the top in a fence on dry ground and exposed to the sun. The new board was placed in the fence 3 weeks before the study was begun, and the old boards above and below the new one were covered along the top edge and the sides by *Placodium microphyllinum*. After 2 years 15 minute areas of the *Placodium* thallus were visible to the eye on the top edge of the new board, the largest area being 1 mm. across. After 3 years hundreds of areas of the thallus were seen scattered over the whole top of the board, some barely visible to the eye, others reaching 0.5 cm. across, while the smallest were visible only under the hand lens. After 4 years the areas of thallus were more numerous and larger, and an examination of the whole length of the board with the hand lens resulted in finding 2 young apothecia, one of them with the disk open. After 6 years the thallus was as abundant and as fully developed on the top edge of the board as on the old boards and could be seen 20 m. distant. There were also a few small areas of the thallus on the sides of the new board near the top edge at this time. The lowest of these was 5 cm. down from the edge. Eleven apothecia were found at this time. After 8 years the apothecia were as frequent on the top edge of the new board as on the old boards. The thallus was not distinctly more abundant on the new board than it was at 6 years.

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[14] See Kentucky, area 28, p. 154.

SUMMARY

One may speculate about possible or probable methods of migration to the denuded quadrats; but nothing is definitely known further than seeing parts of *Cladonia* thalli lying on some of the quadrats in early stages of ecesis. Other possible methods are through fragmentation, through soredia, and through spores. Some probable speculations regarding the means of ecesis might have been made for some of the studies, but this would have been scarcely worth while in the absence of definite data.

Many of the results recorded above cannot be summarized readily, and one must refer to the various studies for such data. Of data which are readily summarizable, the more important are given below.

Graphis scripta increased in diameter from 0.2 to 0.75 cm. in 1 year. *Verrucaria muralis* increased in diameter 0.6 cm. in 1 year. *Physica pulverulenta* increased in diameter for 7 years at the rate of 0.42 cm. per year. *Parmelia borreri* increased in diameter 1.3 cm. in 1 year. *Parmelia caperata* increased in diameter from 0.625 to 1.3 cm. per year for 8 years. *Parmelia conspersa* increased in diameter for 7 years at the average rate of 1.16 cm. per year. *Umbilicaria pustulata* increased in diameter for 8 years at the average rate of 0.36 cm. per year. *Peltigera canina* grew 1.75 cm. in one direction in 1 year.

Biatorella simplex replaced apothecia removed from sandstone conglomerate in 4 years, and sterile *Psora russellii* growing on limestone produced apothecia in the same time. An area of *Peltigera canina* deprived of its apothecia produced 12 young ones in 1 year. Smooth and sterile plants of *Umbilicaria pustulata* growing on high sandstone became strongly pustulate and produced apothecia in 7 years. *Cladonia subsquamosa* on sandstone conglomerate, when deprived of its podetia, regenerated them or produced others in 4 years. The same plant removed from the sandstone conglomerate, except minute fragments, produced squamules of normal size in 4 years and podetia of normal size in 8 years. *Cladonia pityrea* on rails, deprived of its podetia and squamules, except minute fragments, produced normal squamules in 1 year and numerous podetia in 3 years. *Cladonia* *uncialis* in a denuded quadrat on thin soil regenerated new plants of full size in 4 years, from fragments thrown over the quadrat.

Verrucaria nigrescens became established in a denuded limestone quadrat and produced apothecia in 6 years. *Placodium aurellum* became established on limestone and produced apothecia in 4 years. *Placodium microphyllinum* became established on a new plane-tree board in 2 years and produced apothecia in 6 years. *Lecanora dispersa* became established on limestone and produced apothecia in 6 years. *Pyrenopsis schaereri* and *Collema pustulatum* became established on denuded limestone in 8 years, and *Placodium sideritis* became established and produced apothecia in the same time. *Pannaria nigra* became established and produced apothecia on denuded limestone in 7 years. *Endocarpon pusillum* grew and became established and produced apothecia on limestone in 4 years. *Amphiloma lanuginosum* became established on denuded sandstone conglomerate and was plainly visible after 4 years. *Cladonia pyxidata, C. fimbriata,* and *C. mitrula* became established on soil in a denuded quadrat and reached normal size in 5 years. *Cladonia pyxidata* and *C. cristatella* became established on denuded rock and produced podetia and apothecia of normal size in 8 years. *Cladonia subsquamosa* became established on denuded sandstone conglomerate and produced podetia and apothecia of normal size in 8 years.

Certain crustose lichens become established and produce thalli and apothecia in denuded areas in 2 to 8 years. Foliose lichens increase in diameter from 0.3 to 3.5 cm. per year. *Cladoniae* regenerate squamules in one or two years and podetia in 3 or 4 years, and these plants become established by succession in 4 to 8 years.

So far as external appearance goes, lichens produce apothecia in their natural habitats in 1 to 8 years; but, except in instances of primary succession, it is not certain but that the primordia of apothecia were present within the thalli at the time that the various studies given herein were begun. From the studies of primary succession, it would seem that the full development of apothecia to the point when they assume their mature form requires from 4 to 8 years when the plants are growing in their natural habitats.

However, much shorter times have been recorded for development in cultures.

Other similar data could be summarized. However, they would scarcely add to the conclusions regarding the rate of growth and ecesis in lichens, a subject about which so little has been known that one could scarcely form any opinion based on knowledge.

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